On some remarkable new Forms of Caryophyllaeidae from the Anglo-Egyptian Sudan, and a Revision of the Families of the Cestodaria.

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With Plates 24 and 25 and 1 Text-figure.

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INTRODUCTION.

UP to the present time ten more or less well-defined species of the Cestodarian family of the Caryophyllaeidae have been described. These ten species have been named as follows: Caryophyllaeus laticeps (syn. mutabilis, Rudolphi, 1801), Pallas (1781); C. tuba, Wagener (1854); C. fennicus, G. Schneider (1902); C. syrdarjensis, Skrjabin (1913); C. armeniacus, Cholodkovsky (1916); Monobothrium terebrans, Linton (1893); M. hexacotyle, Linton (1898); Glaridacris catostomi, Cooper (1920); Archigetes appendiculatus, Ratzel (1868), and A. brachyurus, Mrázek (1908). Setting aside for the present the question as to whether the first eight of these ten species are rightly to be referred to the three genera named, it is to be remarked that all these ten forms are very similar in their general organization. Apart from minor differences in connexion with the genitalia, more marked differences in the muscular development and shape of the 'head', and the possession of a 'caudal' appendage by Archigetes, all ten species agree in general body-form, in bearing the sexual apertures in the last quarter of the body-length and in therefore having the ovary situated very near to the posterior end, and in the distance between the median 'isthmus' of the ovary and the genital openings being at most (in C. tuba) one-ninth the length of the body (the length of the body being measured from the hind end of the ovary to the anterior extremity in not unduly contracted specimens) and usually much less; also in the presence of a very small group of vitellaria situated posterior to the ovary.

The four new species of Caryophyllaeidae described in the present communication all differ from the ten species above named in at least two of the features just stated, and in three of these new species in all of these features, and since all four species represent marked departures from the type of Caryophyllaeus which, in the form of C. laticeps (Pl. 24, fig. 10), has grown familiar to zoologists, they are of more than usual interest.

My material consisted of specimens, already stained and mounted in balsam, contained in the collection of slides which belonged to the late Dr. A. J. Chalmers when Director of the Wellcome Tropical Research Laboratories at Khartoum, and kindly presented to the Wellcome Bureau by his successor, Major R. G. Archibald. The greater part of this material, though sufficiently well preserved for all ordinary purposes, is yet not good enough for minute histological observations, despite much restaining and section-cutting on my part, and I have therefore omitted descriptions of the finer tissue structures ; I have also omitted to supply the details of structure of such organs as the cirrus and cirrus-sac, the uterus wall, the ovary, testes, and vitellaria, not because it is impossible to do so, but because I do not think that the information thus to be gained is, at least at present, worth supplying,[1] in view of the major differences separating these four new species from all species hitherto described.

Wenyonia virilis, gen. et sp. nov. Woodland, 1923.

Of this species (Pl. 24, figs. 1, 2), the most remarkable in form of the four to be described in this paper and the type species of the new genus, I possess altogether some twenty mature specimens and five small immature specimens. This parasite was found in the Nile Siluroid Synodontis schall, Bloch-Schneider, 1801, common at Khartoum, presumably in the intestine. Two of my specimens are much larger than the remainder, one of the two measuring 52·5 mm. in length with a maximum breadth of 3 mm., and the other (unmeasured and now sectionized) being of about the same dimensions. The other mature specimens range from 11 mm. to 16 mm. in length, with maximum breadths of 1·5 mm. to 1·7 mm. Apart from the difference of size of body and differences in the lengths of the several regions of the body relative to the length of the body as a whole, the two large specimens are identical with the smaller specimens, and I have no reason to believe that the former belong to a distinct species or variety. In shape of body Wenyonia virilis is very constant and characteristic (Pl. 24, fig. 1). The Caryophyllaeid body is usually divided into the three regions : (1) the ' Kopf ' or anterior extremity, usually distinguished from the next region by expansion, form, or muscular differentiation, or all three ; (2) the ' Hals ', the short region intervening between the Kopf and the anterior limit of the testes and vitellaria; and (3) the 'Rumpf' or remainder of the body containing the genitalia; but the so-called neck region is very ill-defined in any species of Caryophyllaeus and ceases to exist when the head is contracted, so that in many cases the body is simply divisible on this system into the head and the trunk regions. Since in W. virilis a new and conspicuous post-ovarian region is developed (Pl. 24, fig. 2)—a region inconspicuous in all previously described Caryophyllaeidae—I propose to dispense with the old 'trunk' region and subdivide the body of W. virilis[1] into the four distinct regions which are obvious even to the naked eye: (1) the head (including the 'neck' when present); (2) the testicular region, extending from the most anterior testes to the genital openings and containing the testes and anterior vitellaria; (3) the dilated and therefore conspicuous uterine region, extending from the genital apertures to the hind end of the ovary and containing the uterus, ovary, shell-gland, ootype, and the middle portions of the two elongated vitellarian strands; and (4) the post-ovarian region (Pl. 24, fig. 2, POVR), composing the rest of the body and containing the posterior more or less scattered vitellaria. The broad ovoid uterine region is plainly visible with the naked eye and is the region of maximum breadth.

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[1] In most cases these inquiries would involve considerable additional section-cutting of somewhat brittle material which has been flattened and preserved in balsam for some years. Should this additional information become necessary in the future, the material is always at hand.

In a specimen measuring 16 mm. in length the head was 2 mm. long and 1·3 mm. broad at the base, the testicular region was 2·2 mm. long and 1 mm. broad, the uterine region 3·5 mm. long and 1·5 mm. in maximum breadth, and the post-ovarian vitellaria extended nearly to the end of the body, i.e. for nearly 8 mm. In my largest specimen (52·5 mm. long, Pl. 24, fig. 1, *a*) the head was 2·1 mm. long and 1·1 mm. broad at the base, the testicular region was 10 mm. long and 2 mm. in maximum breadth, the uterine region 7 mm. long and 2·5 mm. in maximum breadth, and the post-ovarian vitellaria only extended about half-way down the remainder of the body, i.e. for about 16 mm. Thus the ratios of the lengths of the four regions to the length of the body in these two large and small specimens respectively differed considerably, being $\frac{2\cdot 1}{52\cdot 5}$ and $\frac{2}{16}$ for the head, $\frac{10}{52\cdot 5}$ and $\frac{2\cdot 2}{16}$ for the testicular region, $\frac{7}{52\cdot 5}$ and $\frac{3\cdot 5}{16}$ for the uterine region, and $\frac{33\cdot 4}{52\cdot 5}$ and $\frac{8\cdot 3}{16}$ for the post-ovarian region ; but it is noteworthy that the combined lengths of the testicular and uterine regions in each of the two specimens occupied in each case about the same fraction of the body length, i.e. $\frac{17}{52\cdot 5}$ and $\frac{5\cdot 7}{16}$, both of which are roughly equivalent to $\frac{1}{3}$. The head and the tail thus appear to be the variable regions, as might be expected (vide infra).

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[1] This regional subdivision will, of course, apply to the body of all species of Caryophyllaeids.

The head region is very variable in form. Pl. 24, fig. 2, represents what may be regarded as its normal semi-contracted shape, but it can be elongated so that its outline becomes indistinguishable from that of the succeeding testicular region (Pl. 24, fig. 3, *a*, *b*), or, on the other hand, contracted to form a short globular mass (Pl. 24, figs. 3, *d*, *e*, 4). When semi-contracted there is often a short space between the broad base of the ' head ' and the most anterior testes (Pl. 24, fig. 2), but in many cases this space is absent. The surface of the head is marked by deep longitudinal creases lined by thick cuticle (Pl. 24, figs. 2, 3, 5, 6). These longitudinal creases vary in number in different specimens—from 13 or 14 up to 25 or 26—and are perhaps inconstant in the same individual, being dependent upon the contraction of transverse musculature. A transverse section through the base of the head (Pl. 24, fig. 6) shows well-marked longitudinal muscle-fibres scattered throughout the parenchyma between the thick subcuticula and the central muscle-free medullary area, and conspicuous transverse fibres running from side to side : muscle-fibres running obliquely and dorso-ventrally are not conspicuous. The excretory system lies at the base of the subcuticula and not on the edge of the medullary area. A longitudinal section through the contracted head (Pl. 24, fig. 4) shows that the transverse band often visible round and marking the base of the head (as shown in Pl. 24, figs. 2, 3, *a*) is due to a clustering of nuclei probably belonging to muscle-fibres. The two main longitudinal nerves are also seen to unite just below the extreme tip of the head (Pl. 24, fig. 4). I could detect no 'faserzellenstränge', such as have been described by Will (**27**) in C. laticeps, and by Skrjabin (**23**) in C. syrdarjensis.

The testicular region is short relatively to the length of the body as compared with the same region in C. laticeps and other previously described species. It contains a central core of testes (Pl. 24, fig. 2, TES) in, and a thin strand of vitellaria (VIT) on each side of, the central medullary area. The finer branches of the vasa deferentia unite and eventually open into a median main vas deferens (Pl. 24, fig. 7, VDEF) which forms a stout cirrus surrounded by a large cirrus-sac (CIRS). The main vitelline duct lies on the inner side of each strand of vitellaria.

The cirrus opening (Pl. 24, fig. 2, CO) marks the boundary between the testicular and uterine regions. Immediately behind the male aperture lies another and somewhat smaller opening—the vagino-uterine aperture (Pl. 24, figs. 2, 7, VUO)—which, as the name implies, serves both as an entrance to the vagina and as an exit for the eggs from the uterus. An atrium or depression surrounding the two apertures is absent. The vagina (VAG) is a straight or slightly convoluted fairly wide tube which runs in the median line on the ventral side of the body direct from the vaginal aperture to the ovary. Opening into the vagina on its dorsal side and from the right, at a point immediately above the opening of the vagina to the exterior, is the narrowed anterior end of the uterus (Pl. 24, fig. 7, UOP). From the point where it thus opens into the vagina the uterus (UT) curves forward (thus rendering it impossible for the cirrus to enter it) and bends to the left in front of the male aperture, then turns posteriorly and crosses the vagina dorsally to the right, and thence pursues its course posteriorly as the dilated much convoluted canal shown in Pl. 24, figs. 2 and 8. In all of my mature specimens the uterus is full of shell-covered eggs. Posteriorly and immediately in front of the ovary, the vagina develops a slight but constant dilatation, the receptaculum seminis (Pl. 24, fig. 8, RCPS), then inclines to the right, and just below the median isthmus of the ovary dilates into the ootype (OOTP), a large oval chamber which receives the openings of the oviduct (OPO), common vitelline duct (OVIT), and the large shell-gland (SHGL). From the hind end of the ootype arises the uterus (UT) as a slender convoluted duct which, lying dorsal to and to the left side of the median isthmus of the ovary, passes forward and, immediately anterior to the isthmus, turns to the right and commences its zigzag course anteriorly, attaining its wide lumen at a short distance in front of the ovary. The vagina and uterus thus form a complete 'circuit' with a common opening to the exterior anteriorly, the proximal part or vagina serving for the inlet of the spermatozoa and the distal part or uterus serving for the exit of the fertilized eggs. In no other type of Cestode do these two ducts have a common external opening. The ovary or germarium is bipartite and of the form shown in Pl. 24, fig. 2. The two halves are united across the middle line by a transversely elongated receptacle—the isthmus (Pl. 24, figs. 2, 8, IOV)—into each end of which open a number of fine ducts (ODCTS) from one-half of the ovary. In all my mature specimens the isthmus is full of eggs. At the anterior end of the uterine region the mass of testes, divided into two posteriorly in the testicular region by the median vas deferens, ends as two diverging strands, one on each side of the anterior uterus. The marginal strands of vitellaria lie, one on each side, to the outside of the uterus. Pl. 24, fig. 12, represents a transverse section through the uterine region anteriorly, viewed from the hind aspect, in which the uterus (UT, the median space containing two eggs) is seen to be opening into the vagina (VAG, the left extension of the median space, both ducts having a common ventral opening (the vagino-uterine pore, VUO) to the exterior. This transverse section also shows the hind strands of the testicular mass (TES), the vitellaria (VIT) external to these, the two main longitudinal nerve-strands (N), the thick cuticle and subcuticula, the single outer well-defined zone of longitudinal muscle-fibres (LMUS), and the inconspicuous lateral dorso-ventral fibres.

The post-ovarian region—a region which is very short in

C. laticeps and other previously described Caryophyllaeids—is in W. virilis normally extremely long (Pl. 24, fig. 2, POVR) and very characteristic of the species. The only part of the genitalia it contains is an enormous posterior development and extension of the vitellaria (VIT), the two marginal strands of which these organs consist in the uterine and testicular regions here merging immediately behind the ovary into a more or less central core of scattered vesicles. The posterior extension of the vitellaria differs in different specimens. In my largest 52·5 mm. specimen and in a specimen only measuring from 11 to 12 mm. the vitellaria only extend about half-way down the post-ovarian region (Pl. 24, fig. 1, *a*), whereas in most other specimens (Pl. 24, fig. 2) the vitellaria extend nearly to the extreme end, but intermediate conditions doubtless exist, though I do not possess an example. At the extreme posterior end of this region there is developed a distinct muscular thick-walled vesicle (Pl. 24, fig. 2, TEXB), into which open the terminal excretory channels (EXCV).

I must mention finally that in two of my specimens the curious abbreviated condition of the post-ovarian region shown in Pl. 24, fig. 9, was found. This condition may be due merely to extreme local contraction, but since the concentration of the vitellaria hardly seems to be sufficiently great on this supposition, it is possible that in these two specimens the hind end of the animal had become detached during life and a new posterior extremity regenerated on the stump.

A brief description of other features of W. virilis remains to be supplied. The only portions of the nervous system my material allowed me to make out are the two main longitudinal marginal trunks (Pl. 24, fig. 4, N) already described as joining (JN) at the extreme anterior end of the head. I could not detect the other longitudinal nerves which have been described by Will (**27**) in C. laticeps, though possibly restaining of my material by special methods would display them.

The excretory system (Pl. 24, fig. 13) posteriorly was well observed in one of my specimens owing to accidental injection with some foreign substance. It consists at the extreme posterior end of some four or five main longitudinal canals which unite into two or three to open into the excretory bladder (TEXB); more anteriorly these canals apparently branch into ten or more (Pl. 24, fig. 12, EXCV). All these main longitudinal trunks are connected by a network of finer vessels. In the head region (Pl. 24, fig. 6), especially at the base, a large number of peripheral canals are visible under the subcuticula, apparently belonging to a complicated dense network (cf. C. laticeps), and a few canals of about the same size are also visible in the centre of the medullary region, i.e. internal to the zone of longitudinal muscle-fibres. I could observe no distinction between 'ascending' and 'descending' vessels, and my material was not sufficiently well-preserved to allow me to detect flame-cells for certain.

The eggs (Pl. 24, fig. 11) contained in the uterus are ovoid and thin-shelled, and measured, when mounted in balsam, 37·6–41·3 microns in length and 20·1–25·6 microns in breadth. They are thus nearly half the size of the eggs of C. laticeps.

In addition to mature specimens of W. virilis I possess five immature specimens all about 5 mm. in length (Pl. 24, figs. 1, *d*, 14, 15). In the youngest of these (fig. 14) the only signs of developing organs are a strand of thickened tissue with expanded ends (VAGUT) representing the future vagina and uterus (this latter arises as a straight tube), the genital openings and the isthmus of the ovary, and cell-thickenings representing the future testes (TES). In an older stage (fig. 15) the uterus has become convoluted, the genital openings are distinct, the vas deferens is forming, and the rudiments of the vitellaria are apparent. It is noteworthy in these immature specimens that the post-ovarian region is evidently not a mere secondary outgrowth, as is shown by the anterior position of the rudiments of the hind ends of the vagina and uterus. It is also noteworthy that these very immature forms occur in the fish and not in a worm, and that they show no signs of a 'caudal' appendage comparable with that of the larva of C. laticeps. The form of the post-ovarian region in the next two species of Wenyonia to be described clearly proves that this region cannot be homologized with a 'caudal' appendage.

The definitions of the new genus Wenyonia—a genus named in honour of my friend Dr. C. M. Wenyon—and the species W. virilis will be stated below.

Wenyonia acuminata, sp. nov. Woodland, 1923.

Of this species (Pl. 24, figs. 16, 17) I possess four whole specimens, fragments of two others, and a number of longitudinal and transverse sections. The parasite is from the Nile Siluroid Synodontis membranaceus, Is. Geoffr., caught at Khartoum, and was presumably found in the intestine. Thus W. virilis and W. acuminata are found in two closely related species of Synodontis, and it also so happens that these two parasites are also more closely related to each other than to any other species of Caryophyllaeid, as will be evident from the ensuing descriptions. My four whole specimens measured 34·5 mm., 33·0 mm., 26·0 mm., and 17·5 mm. respectively, with corresponding maximum breadths of 1·5 mm., 1·3 mm., 1·2 mm., and 1·2 mm. In all the specimens the greater part of the body was almost uniform in breadth and not unlike that of certain Nematoda, while the head end tapered to a fine point (hence the name of the species) and the posterior extremity was 'stumpy' and bluntly pointed. The maximum breadth of the body occurs, if anywhere, in the testicular region. The head in most of my specimens was not delimited from the rest of the body by any distinct base, though in two of the specimens (Pl. 24, fig. 16) a slight circular ridge or dark band appeared to mark a base, but this I am inclined to think was a transitory contraction, since in both of the specimens possessing a base the anterior testes and vitellaria both extended well anterior to this. In the other four whole specimens (of heads) and in my longitudinal sections the head is quite continuous in outline with the rest of the body (Pl. 24, fig. 17), and I shall consider of course that it ends posteriorly at the point where the anterior testes and vitellaria commence.

In my largest specimen (34·5 mm.) the head measured 3·5 mm. in length, the testicular region 11 mm., the uterine region 13·5 mm., and the post-ovarian region 6·5 mm. In the 26 mm. specimen the head was 4 mm. long, the testicular region measured about 10 mm. long, the uterine region 6·5 mm., and the post-ovarian region 5·5 mm. In the 17·5 mm. specimen the head was 2·5 mm. long, the testicular region 7·5 mm., the uterine region 5 mm., and the post-ovarian region 2·5 mm. There is thus some variation as regards the lengths occupied, relative to the entire body-length, by the several regions.

The head region appears to be practically constant in form and continuous with the testicular region. In transverse and longitudinal sections (Pl. 24, figs. 18, 19) it is seen that the subcuticula is not creased longitudinally, as in W. virilis, both the cuticle and subcuticula being thin. The longitudinal musculature (LMUS) also is not nearly so pronounced as in W. virilis, but, as in W. virilis, consists of a single outer zone. Transverse (TRMUS) and dorso-ventral (DVMS) muscle-fibres are also easily seen.

In the testicular region there is nothing calling for special comment, save that the testes end well in front of the cirrus pore—they do not extend behind as in W. virilis—and that the vitellaria do not extend so far forward as the testes. In some of my preparations the vitelline duct, which lies internal to the vitellaria on each side of the body, is very distinct.

In the uterine region it is seen (Pl. 24, figs. 17, 20) that the uterus is not nearly so voluminous as in W. virilis, and is much shorter, relative to the body-length. The ovary is more attenuated than in W. virilis, and its exact limits are not easy to ascertain; the vitelline strands are also very thin. The detailed conformation of the ducts in the regions of the genital openings and ovary are similar to that found in W. virilis.

The post-ovarian region is much shorter relative to the body-length (Pl. 24, fig. 17) than in W. virilis, and the vitellaria largely retain their marginal strand arrangement, otherwise it is similar to that in W. virilis.

The nervous system is similar to that in W. virilis, so far as the two main longitudinal trunks are concerned. The excretory system is also similar but is much less extensive, especially in the head region, when compared with that of W. virilis. As Pl. 24, figs. 19 and 20 show, there are about ten longitudinal excretory channels underlying the subcuticula and two in the medulla, both at the base of the head and in the uterine region.

The eggs (Pl. 24, fig. 21) are of the usual ovoid shape and measure (when mounted in balsam) 34·7–36·6 microns in length and 21·9–25·6 microns in breadth. They are distinguished from the smooth-surfaced eggs of W. virilis, C. laticeps, the two species yet to be described, and, so far as I know, all other species of Caryophyllaeidae, by the fact that under a magnification of a 1,000 diameters the shell is seen to be covered with minute spines (Pl. 24, fig. 21).

The specific characters of W. acuminata will be stated below.

Wenyonia minuta, sp. nov. Woodland, 1923.

Of this species (Pl. 24, figs. 22, 23) I possess one stained mounted specimen only. Fortunately the specimen is well stained, and I have been able to make out all the main features of its structure without restaining or sectionizing. This parasite was found in the Nile Siluroid Chrysichthys auratus, Günth., at Khartoum, presumably in the intestine. The total length of the body is only 3·5 mm., and the maximum breadth 0·8 mm. It is fully mature, the uterus being filled with eggs. The body is distinctly more flattened than in either of the two preceding species or in C. laticeps, the head is distinctly more of the C. laticeps type, and, as in C. laticeps, the post-ovarian region is short; on the other hand, as in the two preceding species, the genital apertures are situated in the anterior half of the body and the uterus is very long.

The head measured about 0·88 mm., the testicular region about 0·7 mm., the uterine region nearly 1·5 mm., and the post-ovarian region about 0·46 mm.

Notable features concerning the genitalia are (1) the very long uterus, extending over twice the distance covered by the testis mass; (2) the position of the ootype (OOTP) on the left side and the initial coils of the uterus on the right side of the ovary; and (3) the opening of the uterus into the vagina from the left side (Pl. 24, fig. 23, is viewed from the ventral aspect), i.e. exactly the opposite of what occurs in the two preceding species;[1] (4) the breadth of the lateral rows of vitellaria; (5) the extension posteriorly of the testes to about the level of the genital openings; and (6) the apparent anterior extension of the ovary on each side to near the level of the genital apertures (though of this I am not quite certain, owing to the difficulty in my preparation of distinguishing the vitellaria from the ovarian follicles).

The two main nerve-trunks are visible anteriorly, and the excretory opening posteriorly.

The eggs are of the usual ovoid type and measure, when mounted in balsam, 32·9–40·2 microns in length and 20·1–25·6 microns in breadth.

The specific characters of W. minuta will be stated below.

Caryophyllaeus filiformis. sp. nov. Woodland, 1923.

Of this species (Pl. 25, fig. 24) I possess altogether thirty-one entire mounted specimens, and several in transverse and longitudinal sections. This parasite was found in the well-known Nile fish, Mormyrus caschive, L. (a Malacopterygian), at Khartoum, presumably in the intestine. Most of my specimens are mature, and these vary in length from 7·5 mm. to 24 mm. One or two smaller than this (circ. 5 mm.) do not appear to have eggs in the uterus. The usual maximum breadth is 1 mm., but occasionally the body may locally expand to as much as

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[1] I at first concluded that I had viewed the specimen 'wrong way up', but re-examination proves that these statements are correct. I lay no stress on these differences, since it is more than possible that the arrangement of these ducts is variable in different individuals.

2 mm. The general shape of these parasites is indicated in Pl. 25, fig. 24, which in itself provides evidence that the body is very contractile and therefore variable in form and length. In the general topography (Pl. 25, fig. 25) of the genitalia (and in the structural details described below) these parasites are closely related to C. laticeps and other previously described species of Caryophyllaeus, since, as in these species, the genital openings are situated very near to the posterior end and the uterus is therefore relatively very short, and the testes extend over a great length of the body. One feature, however, in which C. filiformis markedly differs from C. laticeps and all other species of Caryophyllaeus is the total absence of vitellaria posterior to the ovary, and of a post-ovarian region, the ovary in most cases extending to the extreme end of the body.

In all specimens of C. filiformis the genital apertures are situated well within the last one-seventh of the body-length (from one-twelfth to one-seventh according to the length of the head). In six typical examples the lengths of the three regions were as follows: in a specimen measuring 21 mm. long, the head measured 10 mm. and the testicular region 9 mm.; in a specimen 23·5 mm. long, the head was 11·5 mm. and the testicular region 10 mm.; in a specimen measuring 21·5 mm. the head was 9 mm. and the testicular region 10·5 mm.; in a specimen measuring 20 mm. the head was 8 mm. and the testicular region 10 mm.; in a specimen measuring 11·5 mm. the head was 5·5 mm. and the testicular region 5 mm.; and in a specimen measuring 15·3 mm. the head was 5·5 mm. and the testicular region 8·3 mm. In five of the specimens (Pl. 25, figs. 26, *c*, *d*) the testes extended much more anteriorly, almost to the extreme front of the head—thus in a specimen measuring 22 mm. the head was only 1·5 mm. long, while the testicular region was 19 mm.—but this is not the normal condition, and intermediate conditions exist between this and the normal.

The head, as already stated, is extremely contractile and assumes the most various shapes (Pl. 25, fig. 26, *a*, *b*, *c*, *d*, *e*). When uncontracted it is fairly flat and ribbon-shaped (Pl. 25, fig. 25), but it may also be pointed (Pl. 25, fig. 26, *c*, *d*) or excessively flattened, with a crenulated margin (Pl. 25, fig. 26, *e*) ; when contracted the head becomes transversely wrinkled and oval in transverse section (Pl. 25, fig. 27) and more robust (Pl. 25, fig. 26, *a*). In transverse section (Pl. 25, fig. 27) it is noteworthy that the longitudinal muscle-fibres are disposed into two distinct zones, an outer peripheral zone (SCLMUS) underlying the subcuticula, and an inner more powerful medullary zone (ILMUS), the two zones being widely separated. This condition of the longitudinal musculature (which is equally well-marked in the testicular region) is also found in C. laticeps, and it differs essentially from the single-zone condition of W. virilis and W. acuminata and probably W. minuta. Some transverse muscle-fibres lie immediately external to the medullary longitudinal musculature. In the anterior head region of some specimens I have observed longitudinal thickenings (Pl. 25, fig. 25) which may be the 'faserzellenstränge' of Will and Skrjabin. I have not examined them in detail.

The testicular region is also remarkable, not only on account of its length relative to the uterine region—a feature in which C. filiformis again resembles C. laticeps—but in the fact that the vitellaria throughout the greater part of this region practically form a ring round the testes, when viewed in transverse section (Pl. 25, fig. 28). In C. laticeps there is an approach to this annular arrangement, but, judging from Will's figures (**27**), it is not nearly so complete as in C. filiformis.

The uterine region (Pl. 25, fig. 29), as already stated, is very short, the uterus itself being short and but loosely coiled. The uterus opens anteriorly into the vagina from the left side (Pl. 25, fig. 25, is from the ventral aspect) and the ootype lies on the left side of the ovary, as in W. minuta. The male and female apertures are more separate from each other than is the case in the preceding species, a space of about 25 microns separating the hind border of the male aperture from the anterior border of the female, and this distance is fairly constant. In

C. laticeps, W. acuminata, and W. minuta the borders of the two apertures are contiguous, as is also usually the case in W. virilis. In all other respects the genitalia of C. filiformis appear to conform to the plan characteristic of Caryophyllaeus.

The two main nerve-trunks (Pl. 25, figs. 25, 27, 28, N) are visible anteriorly, and I have seen them (with difficulty) in my transverse sections.

The excretory channels (Pl. 25, figs. 27, 28, 29) are mostly situated between the inner and outer zones of longitudinal muscles, but a few also occur in the medulla. The vessels cut across in transverse sections form a part of a complicated network, and there appear to be no definite longitudinal vessels; posteriorly, however, some eight or ten longitudinal excretory channels open into the excretory bladder.

The eggs are of the usual ovoid smooth-shelled type and measure, when mounted in balsam, 62·2–69·5 microns in length and 29·2–32·9 microns in breadth, thus being exceptionally long.

The definition of this species, C. filiformis, will be supplied below.

THE GENERA AND SPECIES OF THE CARYOPHYLLAEIDAE.

Skrjabin (**23**) has, with his description of Caryophyllaeus syrdarjensis, included a summary of the small differences which distinguish C. laticeps, C. tuba, C. fennicus, and C. syrdarjensis (all from Cyprinoid fishes) from each other, and C. armeniacus (Cholodkowsky, **2**) only differs from these principally in its large size (55 mm. in length), truncated head, and large eggs (80 × 45 microns). Linton (**10, 11**) has described two other species (also collected from Cyprinidae), which, on account of the form of the head, he refers to Diesing's (**6**) genus Monobothrium,[1] but, excepting for the head, both these species also are essentially identical with the five species of Caryophyllaeus above named. Finally, Cooper (**5**) has described, under the name of 'Glaridacris catostomi', a species (from a Cyprinoid fish) which also 'closely resembles' the aforesaid five species of Caryphyllaeus and the two species described by Linton in general structure, and possesses a 'scolex' which is 'quite similar at least in outward appearance to that of Archigetes brachyurus, Mrázek'. Cooper appears to have been unacquainted with the work of Linton on 'Monobothrium', since he supposes that his 'Glaridacris' is 'the first member of the group [Caryophyllaeidae] to be described from America'. He bases his new genus 'Glaridacris' mainly on the characters of the 'scolex'. Now this 'scolex' of 'Glaridacris', 'when not strongly contracted, has somewhat the form of a truncated rectangular pyramid with the longer diameter in the transverse direction . . . the edges of the base and the apex protrude markedly, in this latter case forming a terminal disc comparable to that of many of the bothriocephalid Cestodes. The dorsal and ventral faces of the organ are each divided by two ridges converging towards the apex into three sucking grooves or loculi, of which the middle is best developed and most efficacious during life. It is also the last to become smoothed out with strong contraction of the whole scolex. The lateral loculi are, furthermore, not in the same plane with the medial one but inclined towards the corresponding ones of the opposite surface so that the edges of the scolex, especially just behind the terminal disc, are often not much thicker than the ridges between the loculi . . . the scolex of this form assumes a greater variety of shapes than that of any other tapeworm I have yet examined, in which respect it is comparable to the leaf-like anterior end of Caryophyllaeus.' From which description and from Cooper's figures, it is evident that the 'scolex' of 'Glaridacris', besides resembling that of Archigetes brachyurus, is extremely similar to the head of Linton's 'Monobothrium hexacotyle', which also has six loculi and a central papilla (' which may project forward as a sharp conical elevation or be contracted to a low eminence') and is similarly 'versatile' in form. If, then, Linton is right in referring his species 'hexacotyle' and 'terebrans' (which latter has a head 'variable, subsagittate, wedge-shape or bluntly rounded') to the genus Monobothrium, it is evident that Cooper's species must likewise be referred to this genus, and 'Glaridacris' becomes a nomen nudum.

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[1] The "Monobothrium serpentum n. sp." of v. Linstow ('Arch. f. Mikr. Anat.', Bd. lxii, 1903, p. 108), 1·4 mm. long, from a cyst in the mesentery of a snake, Patalung, cannot of course be referred to the Caryophyllaeidae. It is almost certainly a Dithyridium larva, several kinds of which have been described from snakes.

The genus Monobothrium was created by Diesing in 1863 (**6**) as one of three genera in his family of the Monobothria, i.e. forms with one 'bothrium'; the other two genera being Caryophyllaeus, Gmelin, and Diporus, Diesing. The genus Diporus can at once be eliminated as solely having reference to the 'Caryophyllaeus trisignatus' of Molin (**14**), a form [1] from the intestine of 'Gadus merlucius' which, in view of Molin's description and figures, cannot be referred with any degree of probability even to the Caryophyllaeidae and much less to any particular genus. The genus Monobothrium, according to Diesing's definition, only differs from Caryophyllaeus in that (*a*) the body is not 'depressum', that (*b*) the head is 'subcylindricum, bothrio, terminali subcirculari' instead of being 'dilatatum fimbriatum, bothrio terminali transverso bilabiato' (definition of Caryophyllaeus head), and that (*c*) the male and female genital apertures open into a common atrium ('apertura genitalis unica') instead of opening separately on the surface ('apertura genitalis feminea pene postposita contigua') as in Caryophyllaeus. Diesing describes two species of Monobothrium—M. tuba (the Caryophyllaeus tuba of Wagener (**15**) and Monticelli (**16**)) from the intestine of Tinca chrysitis, and M. punctulatum, the 'Caryophyllaeus punctulatus' of Molin (**14**) from the intestine of Conger vulgaris—another indeterminate organism described by this author which probably is not even a Caryophyllaeid.

The 'Monobothrium tuba' of Diesing was considered both by Wagener previously and by Monticelli subsequently to belong to the genus Caryophyllaeus, the differences from 'C. mutabilis' (=C. laticeps) only being specific and not generic, and in view of the indefiniteness of such terms as 'subcylindrical' when applied to a pleomorphic structure like the head, of 'depressum' when applied to the body which may be flat anteriorly and oval in section posteriorly even in the same animal, and of 'single' and 'separate' when these refer to genital apertures which show all degrees of opening into a common atrium in different species which undoubtedly are to be included in one genus, it is impossible not to agree with Wagener and Monticelli. Further, as is demonstrated in the present communication, the muscular cylindrical type of head, which was the most characteristic feature of Diesing's genus Monobothrium, is to be found associated, indiscriminately, with two very different types of body, whence it is evident that the character of the head cannot serve in this group as a feature of generic value. The name Monobothrium thus also lapses.

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[1] Possibly a Tetrabothriid scolex, as Monticelli suggests.

Having thus concluded that eight of the ten Caryophyllaeid species described previously to this communication belong to the genus Caryophyllaeus, and provisionally allowing Archigetes to stand as a separate genus on the sole ground that it possesses a 'caudal' appendage in the sexual condition, it is necessary to redefine the genus Caryophyllaeus and to show reason for creating a new third genus, Wenyonia.

The genus Caryophyllaeus was apparently founded by O. F. Müller in 1787 (**18**), but since I have not been able to consult this work I will give the definition of this genus supplied by Gmelin (**7**) in 1790, which is probably fully as comprehensive as that of Müller, both being based on specimens of C. laticeps. Gmelin's definition of the genus is: 'Corpus teres: ore fimbriato. . . . Habitat in piscium, aquas dulces inhabitantium, potissimum cyprinorum, carpionis, tincae, jesis, bramae intestinis, rarior, margaritaceus, ad pollicem longus, reliquis intestinalibus vitae tenacior, fine posteriori rotundato, anteriori latiori.' This definition clearly applies to C. laticeps, but it is too special to include other species subsequently described, and Diesing (**6**) therefore, as aforesaid, created another genus—Monobothrium—to include the 'Ligula tuba' of Wagener (**25**) and the 'Caryophyllaeus punctulatus' of Molin. Diesing's definitions of the two genera Caryophyllaeus and Monobothrium are respectively as follows: 'I. Caryophyllaeus, Gmelin. Corpus continuum elongatum depressum, vesicula pulsatoria postica cum poro excretorio. Caput dilatatum fimbriatum, bothrio terminali transverso bilabiato. Os . . . Collum nullum. Penis lateralis conicus retractilis retro medium corporis; apertura genitalis feminea pene postposita contigua. In Piscium fluviatilium praeprimis Cyprinorum intestinis. Evolutio directa.' [One species C. mutabilis, Rud.], and 'II. Monobothrium, Diesing. Corpus continuum elongatum, vesicula pulsatoria postica, caput sybcylindricum, bothrio terminali subcirculari. Os . . . Collum nullum. Apertura genitalis unica, organo musculo et femineo communis, lateralis ventralis in postico corporis triente. In Cyprinorum intestinis. Evolutio ignota. (Animalcula bothrii ope parieti intestini firmiter adhaerent. Systema vasorum e truncis longitudinalibus quatuor et vasculorum rete compositum).' [Two species: M. tuba, Wagener. and M. punctulatum, Molin.] Other and more recent authors, e.g. Lühe (**13**) and Cholodkowsky (**3**), group the species of the Caryophyllaeidae into two genera—Caryophyllaeus and Archigetes—and distinguish the former from the latter chiefly by the absence of the 'caudal' appendage in the sexual stage of the former.

Assuming the definition of the Caryophyllaeidae to be that which I shall propose in the next section, I now propose to divide these forms into three genera—Caryophyllaeus, Archigetes, and Wenyonia—with the following definitions:

Caryophyllaeus, O. F. Müller, 1787 emend.

The sexual apertures are situated within the last quarter of the body-length, and the ovary is near the posterior extremity. The longitudinal extent of the uterus is at most one-third of that of the testes and usually much less.[1] Parasitic in the intestines of Malacopterygii and Ostariophysi (Cyprinidae, Mormyridae, and Siluridae[2]).

Archigetes, Leuckart, 1878.

The sexual apertures are situated within the last quarter of the body-length; and the ovary is near the posterior extremity. The longitudinal extent of the uterus is at most one-third of that of the testes and usually much less. The body of the mature parasite possesses a 'caudal' appendage posteriorly. Parasitic in the body-cavity of aquatic Oligochaetes.

Wenyonia, Woodland, 1923.

The sexual apertures are situated in the anterior half of the body. The longitudinal extent of the uterus is at least equal to that of the testes. Parasitic in the intestine of Siluridae.

The species known up to the present contained in these three genera are as follows :

C. laticeps, Pallas, 1781.

Length of body 11–30 mm. ; breadth of body 0·5–2 mm. Body posterior to the head oval in transverse section. Hind end bluntly pointed or rounded. Head region flattened, usually broader than the body and with fimbriated edges, but very contractile and variable in form; longitudinal grooves absent on head. Genital apertures in last fifth of body-length.[1] Post-ovarian vitellaria are present. Eggs measure about 66 microns in length. Parasitic in intestine of Cyprinidae, Europe.

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[1] With the single exception of Linton's 'Monobothrium hexacotyle' (C. hexacotyle), which has eggs measuring only 38–40 microns in length, all species of Caryophyllaeus, as enumerated further in the text, possess eggs about 60 microns in length, or, as in the huge C. armeniacus, 80 microns in length. On the other hand, in all three species of Wenyonia the eggs average from 32 to 40 microns in length. These differences are remarkable (especially in view of the body-sizes of the parasites) and may possess a classificatory value. Another difference which may distinguish these two genera is that in Wenyonia the longitudinal muscles are solely contained in a peripheral subcuticular zone, whereas in Caryophyllaeus the longitudinal muscles are disposed in two zones—a subcuticular and an epi-medullary.

[2] I include this family because of the immature species of Caryophyllaeus found by me in Auchenoglanis occidentalis and described briefly at the end of this paper.

C. tuba, Wagener, 1854 ('Monobothrium tuba').
Length of body 10–30 mm.; breadth of body 0·9–1 mm. Body and head oval in transverse section. Hind end slightly tapering and pointed. Head 'stumpy', i.e. bluntly rounded in outline and not broader than body; longitudinal grooves absent on head. Genital apertures situated anterior to the last fifth of the body.[2] Post-ovarian vitellaria are present. Eggs? Parasitic in intestine of Tinca chrysitis, Italy.

C. fennicus,[3] Schneider, 1902.
Length of body 5–9·5 mm.; breadth of body 0·4–0·5 mm. Body and head somewhat flat in transverse section. Hind end bluntly pointed. Head rounded in contour and not broader than body; longitudinal grooves absent on head. Genital apertures as in C. laticeps. Post-ovarian vitellaria present. Eggs measure about 60 microns in length. Parasitic in intestine of Leuciscus erythrophthalmus, Finland.

C. syrdarjensis, Skrjabin, 1913.
Length of body 6·3–16 mm.; breadth of body 1–1·5 mm. Body and head somewhat flat in transverse section. Hind end bluntly rounded. Head slightly flattened and slightly broader than body, with distinct 'faserzellenstränge'; longitudinal grooves absent on head. Genital apertures apparently as in C. laticeps. Post-ovarian vitellaria are present. Eggs measure about 63 microns in length and 48 microns in breadth. Parasitic in intestine of Schizothorax intermedius, Russo-Turkestan.

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[1] Statement based on measurements of four individuals in my possession.

[2] Statement based on the figures supplied by Monticelli (**15**) and Wagener (**25**).

[3] Skrjabin (**23**) is mistaken in supposing that in C. fennicus alone do the coils of the uterus ever extend anterior to the vagino-uterine aperture: I have seen this anterior extension in at least two specimens of C. laticeps (Pl. 24, fig. 10).

C. armeniacus, Cholodkowsky, 1915.

Length of body reaches 55 mm., with breadth of 5 mm. Body and head oval in transverse section. Hind end slightly tapering and bluntly pointed. Head not broader than body, truncated, with wedge-shaped anterior extension; longitudinal grooves absent on head. Genital apertures in last fifth of body-length. Post-ovarian vitellaria are probably present. Eggs about 80 microns long and 45 microns broad. Parasitic in intestine of Capoeta sp., Armenia.

C. terebrans, Linton, 1893 ('Monobothrium terebrans').

Length of body reaches 28 mm., with breadth about 2·5 mm. Body oval in transverse section. Hind end dilated at level of sexual apertures and pointed posteriorly. Head broader than body and subsagittate, wedge-shaped or bluntly rounded; longitudinal grooves absent. Genital apertures at about the anterior limit of the last fifth of the body. Post-ovarian vitellaria are present. Eggs measure 60–65 microns in length and 30–35 microns in breadth. Parasitic in intestine of Catostomus ardens, Wyoming, U.S.A.

C. hexacotyle, Linton, 1898 ('Monobothrium hexacotyle').

Length of body reaches 14·5 mm., with breadth of 1 mm. Body oval in transverse section. Hind end tapering and pointed. Head not broader than body, broad at base, pointed anteriorly and wedge-shaped, each of the dorsal and ventral surfaces of the wedge bearing three broad elongated loculi or triangular grooves which point to the anterior extremity; shape variable. Genital apertures in last fifth of body-length. Post-ovarian vitellaria are present. Eggs measure 38–40 microns in length and 20 microns in breadth. Parasitic in the intestine of Catostomus sp., Arizona, U.S.A.

C. catostomi, Cooper, 1920 ('Glaridacris catostomi').

Length of body measures 5–25 mm., with maximum breadth 0·4–1 mm. Body oval in transverse section. Hind end tapering and pointed. Head region broader than body, and similar in shape to that of Archigetes brachyurus, i.e. wedge-shaped, the dorsal and ventral surfaces of the wedge each bearing three broad loculi, the end of the wedge being truncated when viewed dorsally or ventrally but pointed in lateral view ; shape variable. Genital organs 'like those of Caryophyllaeus'. Post-ovarian vitellaria present. Eggs measure 54–66 microns in length and 38–48 microns in breadth. Parasitic in the intestine of Catostomus commersonii, Michigan, U.S.A.

C. filiformis, Woodland, 1923.

Length of body measures 7·5–24 mm., with breadth (maximum) 1–2 mm. The body is broadest in its posterior half, the anterior half (or third) being attenuated and usually filiform or ribbon-shaped ; the body posterior to the head region is oval in transverse section. The hind end of the body is bluntly rounded. The head region is highly contractile, is more or less pointed in front, is narrow, always more flattened than the body posteriorly, and varies in form from a thin pointed filament or ribbon to a tapering wrinkled digitiform structure ; longitudinal grooves are absent. Genital apertures in last seventh of the body-length ; the cirrus aperture is distinctly separated from the vagino-uterine aperture, and there is no atrium. Post-ovarian vitellaria are entirely absent. Eggs (in balsam) measure 62·2–69·5 microns in length and 29·2–32·9 microns in breadth. Parasitic in the intestine of Mormyrus caschive, L., Anglo-Egyptian Sudan.

Archigetes appendiculatus, Ratzel, 1868, and A. brachyurus, Mrázek, 1908.

Both of these species possess 'caudal' appendages, the former an appendage about equal in length to the rest of the body, the latter an appendage only about one-sixth the length of the rest of the body. A. appendiculatus varies from 2·5 to 3 mm. in length, and is parasitic in the body-cavity of Limnodrilus hoffmeisteri and Tubifex rivulorum, Europe ; A. brachyurus is 5–6 mm. long and is also parasitic in the body-cavity of Limnodrilus hoffmeisteri. The genital organs of these two species apparently resemble those of Caryophyllaeus.

Wenyonia virilis, Woodland, 1923.

Length of body varies from 11 to 52·5 mm. and maximum breadth from 1·5 to 3 mm. The body is externally divisible into four distinct regions—a broad-pointed head region, a narrow elongated testicular region, a dilated uterine region, and a normally long narrow tapering post-ovarian region ; the body and head are oval in transverse section. The testicular and uterine regions, which are roughly equal in length, together occupy about one-third of the total body-length. The post-ovarian region is at least equal in length to the combined testicular and uterine regions. The hind end of the body gradually tapers to a fine point. The head region is normally sagittate in form, its base only being slightly broader than the testicular region, is oval in transverse section, highly muscular, and bears thirteen to twenty-six deep longitudinal grooves which are not suctorial or fixative in function ; highly contractile. Post-ovarian vitellaria about equal, as regards area covered, to the anterior vitellaria. Eggs (in balsam) measure 37·6–41·3 microns in length and 20·1–25·6 microns in breadth, thus being very small compared with eggs of Caryophyllaeus. Parasitic in intestine of the Siluroid Synodontis schall, Anglo-Egyptian Sudan.

Wenyonia acuminata, Woodland, 1923.

Length of body varies from 17·5 to 34·5 mm. and maximum breadth (in testicular region) 1·2 to 1·5 mm. The body is not externally divisible into regions but is nematodiform and oval in transverse section. The testicular and uterine regions, which are roughly equal in length, together occupy about two-thirds of the total body-length. The post-ovarian region is never more than one-third the length of the combined testicular and uterine regions, and is usually less. The hind part of the body only slightly tapers and ends in a blunt point. The head region is tapering and finely pointed and narrower than the testicular region ; it is not highly muscular, not specially contractile, and bears no longitudinal grooves. The post-ovarian vitellaria are not so numerous as the anterior vitellaria. Eggs (in balsam) measure 34·7–36·6 microns in length and 21·9–25·6 microns in breadth, and are distinguished from the eggs of all other (at present) known Caryophyllaeidae by the egg-shell being covered with minute spinelets. Parasitic in the intestine of Synodontis membranaceus, Anglo-Egyptian Sudan.

Wenyonia minuta, Woodland, 1923.

Length of body about 3·5 mm. and breadth 0·8 mm. The body is fluke-like in form, being flat, oval in outline, and with bluntly pointed extremities. The uterine region is at least twice the length of the testicular region and the two regions together occupy about two-thirds of the entire body-length. The post-ovarian region is inconspicuous. The head region is, like the posterior regions, flattened, and much narrower than the body, is bluntly pointed, with irregular edges—in fact Caryophyllaeiform; it bears no longitudinal grooves and is very contractile. The post-ovarian vitellaria form a small group continuous with the anterior broad marginal strands. Eggs (in balsam) measure 32·9–40·2 microns in length and 20·1–25·6 microns in breadth. Parasitic in the intestine of the Siluroid Chrysichthys auratus, Anglo-Egyptian Sudan.

On the Caryophyllaeidae, Gyrocotylidae and Amphilinidae, and Cestodaria in general.

Having re-defined the genera of the Caryophyllaeidae, it is necessary to re-define the family, since previous definitions not only alone refer to Caryophyllaeus and Archigetes forms, but appear to me to be defective in emphasizing some of the more important features displayed by these genera.

The family was apparently first defined, with some degree of precision, by Claus in 1885 (**4**), stress being laid upon the elongated, unsegmented body, wrinkled anterior border, absence of hooks, eight or more main excretory canals, the general features of the genital apparatus and simple development, and subsequent authors have not improved upon this definition to any extent. In re-defining the Caryophyllaeidae we have to distinguish them from the two other families of the Cestodaria, viz. the Gyrocotylidae and Amphilinidae, and therefore the features to be emphasized are that the body is usually not flattened to the extent that the Cestode strobila is, that calcareous corpuscles are entirely absent, that they never possess true circular suckers, that sucking grooves or bothria may be present (always different in number, form, and arrangement to those found in merozoan Cestoda) in some forms (C. catostomi, C. hexacotyle, and Archigetes brachyurus), that the vagina and uterus form a complete circuit with a single common opening to the exterior, that the arrangement of the genitalia is very distinctive, and that the larva of some species is hexacanth. Taking these features into account, the Caryophyllaeidae may be defined as

> Cestodaria, usually with a slightly flattened cylindrical elongated body but sometimes fluke-shaped, devoid of calcareous corpuscles and cuticular spinelets or hooks, with an anterior end extremely variable in form and size, both in the individual and in different species, which never carries circular suckers but may bear shallow elongated grooves (different in number, form, and arrangement to those found on the scolex of other Cestoda), with the cirrus and vagino-uterine apertures contiguous or nearly contiguous on the ventral surface of the body in the median line and occasionally opening into a common shallow atrium, with the testes situated anteriorly and entirely in front of the uterus, with the vagina and uterus forming a complete circuit with a common vagino-uterine opening to the exterior, with a network of excretory channels, the larger ones of which form irregular longitudinal canals about eight or ten in number and all of which open externally by a median posterior excretory bladder, and with a larval form known in some cases to be hexacanth. Parasitic in the intestine of Teleostome fishes (Malacopterygii and Ostariophysi) and in the body-cavity of aquatic Oligochaeta (Tubificidae).

Re-definition of the Caryophyllaeidae necessitates re-definitions of the other two families of the Cestodaria. The Gyrocotylidae, comprising four species of the well-known genus Gyrocotyle (**24, 8, 26**), may be defined as

> Cestodaria with a flattened elongated body, devoid of calcareous corpuscles but possessing cuticular spinelets, with an anterior ovoid sucker and a posterior 'rosette' in all known forms, with the cirrus and vaginal apertures adjacent but not contiguous, and situated anteriorly on the left margin of the body, with the testes situated anteriorly and to the outer sides of the median uterus, with the uterine aperture situated anteriorly on the ventral surface in or near the median line, a short distance but quite separate from the vaginal aperture, with a close network of fine excretory vessels devoid of main longitudinal

> channels and not opening by a posterior vesicle, and with typical hexacanth larvae in some species but in others a ten-hooked larva similar to that of Amphilinidae. Parasitic in the intestine of Holocephali.

The Amphilinidae[1] may be re-defined as

> Cestodaria with a flattened more or less elongated body, possessing calcareous corpuscles but devoid of cuticular spines and hooks, with a large anterior boring apparatus (proboscis, boring muscle and anchor cells) but devoid of suckers and bothria, with the cirrus and vaginal apertures either in close apposition or only separated by a short distance, both situated posteriorly on or near the edge of the hind end of the body, with the testes extending over, with the uterus, the greater length of the body, usually as two marginal rows lying external to the coils of the uterus but sometimes more scattered, with the vagina lying posterior to the ovary and the uterus anterior, with the uterine opening at the extreme anterior end, with a very long uterus, consisting of three limbs disposed like the letter N when viewed ventrally, with two main lateral longitudinal excretory channels opening medianly at the posterior extremity, and with a larval form possessing ten hooklets. Parasitic in the body-cavity of Acipenseridae, Osteoglossidae (Arapaima), Haemulidae (Diagramma), and Siluridae (Macrones).

Comparing these three families, it appears to me self-evident that the Caryophyllaeidae and Gyrocotylidae are much more closely allied to each other than is either of these families to the Amphilinidae. In both of the former families (*a*) the three sexual apertures are all grouped together, and at least two of them (the uterine and vaginal) are, in both families, situated on the (ventral ?) surface in or near the median line and not on the edge of the body ; (*b*) in both families the uterus and vagina run parallel to and in the same dorso-ventral plane with each other along the longitudinal axis of the body, and in both the testes occupy only the anterior end of the body ; (*c*) in both families the ovary is bipartite, and (*d*) in both calcareous corpuscles are absent ; (*e*) in both families hexacanth embryos have been found ;[1] and (*f*) a reticulate type of excretory system is common to both. On the other hand, in the Amphilinidae, (*a*) the uterine and vaginal apertures are situated at opposite ends of the body and are in all cases situated on or near the body edge ; (*b*) the uterus and vagina run in opposite directions from the ovary, the former anteriorly and the latter posteriorly ; (*c*) the ovary is unipartite ; (*d*) calcareous corpuscles are present ; (*e*) hexacanth larvae have not been found, the larva being of the ten-hooked kind ; and (*f*) the excretory system consists of two main longitudinal canals only and minor regularly arranged looped canals. I am thus unable to agree either with Monticelli (**15**) in believing that Amphilina and 'Amphiptyches' (Gyrocotyle) are closely related forms, or with Lönnberg (**12**), who is of opinion that the Caryophyllaeidae differ essentially from the Gyrocotylidae in being secondarily monozoic forms, the Gyrocotylidae being, in his opinion, primarily monozoic. I cannot find that either of these authors have advanced any valid reasons for these opinions. It is true that Gyrocotyle differs from all Caryophyllaeidae in possessing an anterior sucker and a posterior 'funnel' (with muscular and nervous modifications to match), but the extremities of these animals can develop almost any kind of process, as we see in the Caryophyllaeidae, and this difference, as also the minor differences in the conformation of the genitalia and in

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[1] See the writer's paper on Amphilina paragonopora recently published in this journal (**28**). I may remark in this place that Poche's paper "Zur Kenntnis der Amphilinidea" ('Zoologischer Anzeiger', Bd. liv, 1922, p. 276) appeared too late for me to refer to it in my own paper, and that I am wholly unable to concur with the author's grotesque proposal to found separate families and sub-families for known species of Amphilina. The best policy to adopt with suggestions of this kind is to ignore them.

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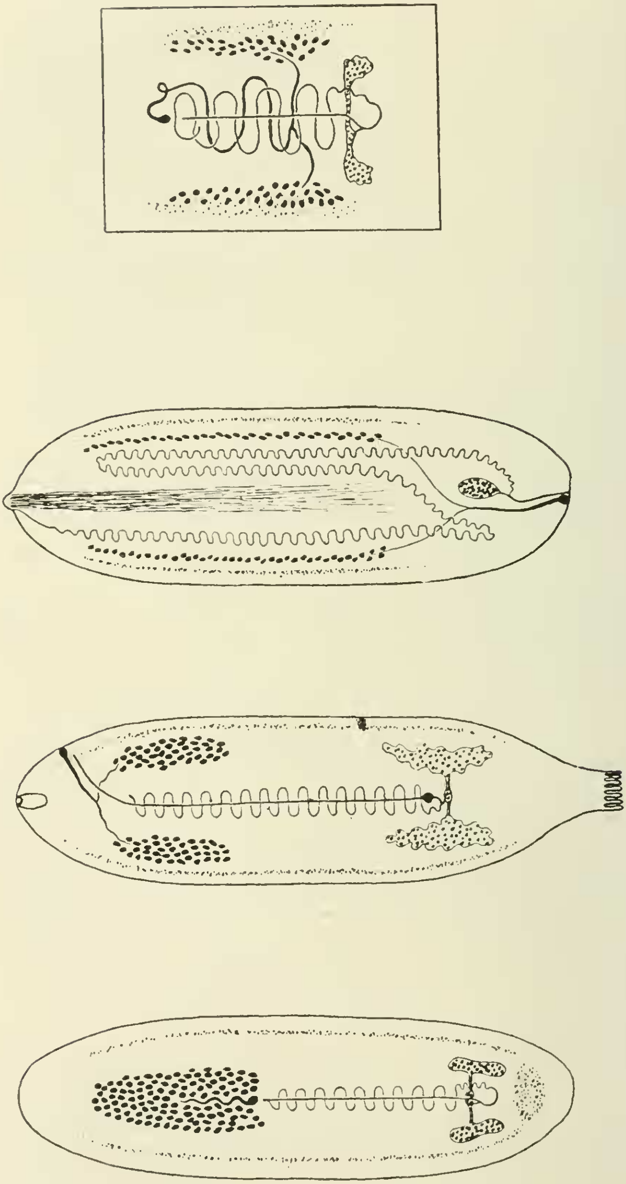
[1] Both Spencer (**24**) and Hungerbühler (**9**) found in certain species of Gyrocotyle ten-hooked larvae similar to those of Amphilina, while in G. urna Lönnberg ('Biol. Fören. Förhandl., Verhandl. d. biol. Ver. in Stockholm', vol. ii, 2, p. 55, 1890) found larvae apparently altogether devoid of hooks. The significance of these facts is as yet obscure.

TEXT-FIG.



To illustrate the orientation and disposition of the genitalia in the three families of the Cestodaria and in the Bothriocephalidae.

the excretory system, cannot be considered of much weight when the fundamental resemblances I have indicated are taken into consideration. I therefore propose, in order to emphasize these fundamental resemblances, provisionally to unite the Caryophyllaeidae with the Gyrocotylidae into one Order, the Paralinidea, in contradistinction to the Amphilinidea, which contains only one known family,[1] the Amphilinidae.

The Paralinidea may be provisionally defined as

> Cestodaria (*a*) with the three sexual apertures situated close together; (*b*) with the uterus and vagina running parallel to each other in the same dorso-ventral plane along the median longitudinal axis of the body; (*c*) with the testes restricted to the anterior end of the body; (*d*) with a bilobed ovary; (*e*) without calcareous bodies; (*f*) with a reticulate excretory system; (*g*) with a hexacanth larva (?).

The Amphilinidea possess the opposite characters, viz.

> (*a*) the uterine and vaginal apertures are situated at opposite ends of the body, the former being at the anterior and the latter posterior; (*b*) the uterus and vagina run in opposite directions from the ovary, the former anteriorly and the latter posteriorly; (*c*) the testes extend, with the uterus, over the greater length of the body; (*d*) ovary one-lobed; (*e*) calcareous corpuscles present; (*f*) excretory system consisting of two main lateral longitudinal channels with minor regularly arranged looped vessels; (*g*) with a ten-hooked larva.

Finally, it is evident that of the two Cestodarian Orders—Amphilinidea and Paralinidea—the latter is much more closely related to the Cestoda merozoa than is the former (Text-fig.). In both the Paralinidea and the Bothriocephalidae the uterus and the vagina run medianly in the same dorso-ventral plane, the vas deferens opens from the anterior side of the proglottis (though the testes are necessarily displaced from their primitive anterior position), the three sexual apertures are all close together, the ovary is bipartite, and a hexacanth larva is present.

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[1] Benham (1) would place Wageneria in this Order, but this organism is not yet known with sufficient accuracy to justify its inclusion in any family.

I would not, however, go so far at present as to follow Lühe (**13**) in actually grouping the Caryophyllaeidae with the Diphyllobothriidae in his Order Pseudophyllidea, because for me the monozoan character of the Paralinidea is a fundamental one, and to me it is inconceivable that the Paralinidea have become secondarily monozoan. It is also well to remember that the Amphilinidea may not be so far removed from the Paralinidea as their existing structure would seem to indicate, for the simple reason that this structure is, in part at least, an obvious adaptation to the mode of life of Amphilina. Amphilina is parasitic in the body-cavity and not the gut of the fish, and it can only liberate its larvae to the external world by boring through the body-wall of its host (hence the huge boring apparatus I have described (**28**) and the extreme anterior position of the uterine pore) and has to retain its larvae until it has penetrated to the outside of the fish (hence its enormously elongated uterus—a duct which would not need to be so elongated if, as in the Paralinidea, the parasite could continually shed its eggs into the intestine). These bionomic necessities must have caused a great transformation in the entire anterior end of the animal and especially in the arrangement of all the contained ducts, and it is therefore possible that even the posterior position of the vas deferens and the vagina (the openings of which must remain adjacent) is to be regarded as but another indirect concomitant of the general rearrangement. In other words, the original plan of the genitalia in Amphilina is possibly largely masked by specialization and, in the light of present knowledge, it may be incorrect to conclude that Amphilina is more separate genetically[1] from the Paralinidea than these are from the merozoan Cestodes. However, I concede that it is possible that this conclusion may prove to be the correct one and that, as several authors have supposed, the ' Cestodaria ' may be polyphyletic in origin.

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[1] The fact that in both the Paralinidea and Amphilinidea ten-hooked larvae have been found may be called to mind in this connexion. I may here remark that Sanguinicola (still included in 1916 by Cholodkowsky (3) in the Cestodaria) is now known not to be a Cestode :

ON AN IMMATURE CARYOPHYLLAEUS SP. FROM THE INTESTINE OF AUCHENOGLANIS OCCIDENTALIS, CUV. AND VAL., 1840.

I possess a single specimen of a species of Caryophyllaeus (Pl. 25, fig. 31) which is immature and which was found in the intestine of the Siluroid Auchenoglanis occidentalis at Khartoum, Anglo-Egyptian Sudan. The specimen measures 2 mm. in length and about 0·5 mm. in maximum breadth (posteriorly). The body is relatively thick and has the wrinkled appearance shown in Pl. 25, fig. 32. I cut this specimen into horizontal longitudinal sections and discovered that its internal structure was on the same general plan as that of C. filiformis. The ovary and vitellaria were still rudimentary, though the uterus, vas deferens, and their openings were well defined. The testes were not fully developed. Apparently the vagina was convoluted in form and not straight as is usual, and it was not easily distinguishable in sections from the uterus.

In conclusion, I wish to express my thanks to Dr. Andrew Balfour, Director of the Wellcome Bureau, for the opportunity of examining the interesting new forms of Caryophyllaeidae above described, to Professor J. P. Hill for the loan of five specimens of Caryophyllaeus laticeps, and to Mr. C. A. Hoare for his kind aid in translating certain passages in Russian.

SUMMARY.

1. Four remarkable new species of Caryophyllaeidae from the Anglo-Egyptian Sudan are described, three of which (from Siluroid fishes) are referred to a new genus, Wenyonia —W. virilis, W. acuminata, and W. minuta—and the fourth (from Mormyrus caschive) to the original genus

vide my paper on this form in the present volume of the ' Quart. Journ. Micr. Sci.'

Caryophyllaeus—C. filiformis. The chief characteristics of the new genus are the situation of the sexual apertures in the anterior half of the body, and the elongated uterus. The family Caryophyllaeidae, after deletion of the genera Diporus, Monobothrium, and Glaridacris, thus contains three genera—Caryophyllaeus, Archigetes, and Wenyonia—all of which are re-defined, with their known species.

2. Very young immature forms of Wenyonia occur in the same (Siluroid) host as the adult and are devoid of a 'caudal' appendage, whence it would appear that the life-history of these new forms is different from that of C. laticeps.

3. The three families of the Cestodaria—Caryophyllaeidae, Gyrocotylidae, and Amphilinidae—are re-defined.

4. The Cestodaria, after eliminating Sanguinicola (a Trematode ?), are provisionally grouped into two Orders: the Amphilinidea (with one family, the Amphilinidae) and the Paralinidea (with two families, the Caryophyllaeidae and the Gyrocotylidae), the latter being closely allied to the Bothriocephalidae. These two Orders are defined.

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DESCRIPTION OF PLATES 24 AND 25.

REFERENCE LETTERS.

BH, base of head ; CIRS, cirrus sac ; CO, cirrus opening ; DVMS, dorsoventral muscle-fibres ; EXCV, excretory vessels ; FZS, ' Faserzellenstränge ' ? ; H, head region ; ILMUS, internal layer of longitudinal muscle-fibres on edge of medulla ; IOU, isthmus of ovary ; JN, junction of the two main longitudinal nerve-trunks anteriorly ; LCH, longitudinal creases or grooves in subcuticula of head ; LD, local dilatation ; LMUS, longitudinal muscle-fibres ; M, medulla ; N, main longitudinal nerve-trunk ; NT, nuclear thickening at base of head ; ODCTS, ducts from ovary opening into isthmus ; OOTP, ootype ; OPO, opening of oviduct into ootype ; OV, ovary ; OVD, oviduct ; OVIT, opening of vitelline duct into ootype ; POVR, post-ovarian region ; RCPS, receptaculum seminis ; SCLMUS, outer layer of longitudinal muscle-fibres underlying subcuticula ; SHGL, shell-gland ; TES, testes ; TEXB, terminal excretory bladder ; TRMUS, transverse muscle-fibres ; UOP, opening of uterus into vagina ; UT, uterus ; VAG, vagina ; VAGUT, rudiment of vagina and uterus ; VDEF, vas deferens ; VIT, vitellaria ; VITD, vitelline duct ; VUO, vagino-uterine opening.

N.B.—The magnifications given are those at which the figures were drawn. The 5 cm. scales provided on the two plates show, when compared with an actual 5 cm., the amount of reduction[1] which has occurred in reproducing the figures. All figures drawn by means of the camera lucida.

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[1] Approximately $\frac{11}{25}$.

Plate 24.

Wenyonia virilis.

Fig. 1, *a*, *b*, *c* (×2).—Adult specimens as mounted on slides and probably somewhat flattened.

Fig. 1, *d* (×2).—Three immature specimens.

Fig. 2 (×24).—Entire specimen magnified (the two halves of the figure should be continuous) and viewed from the dorsal aspect. The parts of the drawing round the sexual openings and the ovary have been made somewhat diagrammatic for the sake of clarity, and the uterus is in actuality full of eggs. The vitelline and other fine ducts are not shown.

Fig. 3, *a*, *b*, *c*, *d*, *e* (×24).—Figures showing the variations in form of the head region.

Fig. 4 (×35).—Horizontal section through a much contracted head.

Fig. 5 (×35).—Transverse section through the anterior region of the expanded head to show the longitudinal grooves (the thick cuticle and excretory channels are not indicated).

Fig. 6 (×78).—Transverse section through the posterior region of the head to show the longitudinal grooves, musculature and excretory network (thick cuticle not shown).

Fig. 7 (×112).—Ventral aspect of the genital openings and associated ducts.

Fig. 8 (×175).—Dorsal aspect of the ducts in the region of the ovary in outline.

Fig. 9 (×24).—The abbreviated (contracted? regenerated?) post-ovarian region in one of the two specimens showing this feature.

Caryophyllaeus laticeps.

Fig. 10 (×9).—C. laticeps from Tinca vulgaris, from the dorsal aspect (for comparison with Wenyonia spp.). The structures in the regions of the sexual apertures and ovary are represented somewhat diagrammatically, but the figure is otherwise correct. In most specimens of C. laticeps, however, the uterus does not extend anteriorly to the cirrus opening, at least to any extent.

Wenyonia virilis.

Fig. 11 (×1060).—Egg (contained in the uterus).

Fig. 12 (×78).—Transverse section through the uterine region, viewed from the front aspect, showing the vagino-uterine aperture.

Fig. 13 (×78).—The posterior excretory system artificially injected.

Figs. 14, 15 (×24).—Immature specimens showing developing genitalia.

Wenyonia acuminata.

Fig. 16 (×2).—Adult specimens (the dilated base of the head shown in two of the specimens is probably not a constant feature).

Fig. 17 (×9).—Entire specimen magnified and viewed from the dorsal aspect. The parts of the drawing round the sexual openings and the ovary have been made somewhat diagrammatic for the sake of clarity and the uterus is in actuality full of eggs. The vitelline and other fine ducts are not shown.

Fig. 18 (×55).—Longitudinal vertical section through head.

Fig. 19 (×55).—Transverse section through the anterior end of the testicular region.

Fig. 20 (×55).—Transverse section through the middle of the uterine region.

Fig. 21 (×1060).—Eggs in optical section and surface-view to show the minute spinelets on the shell.

Wenyonia minuta.

Fig. 22 (×2).—The adult specimen.

Fig. 23 (×60).—The entire specimen magnified and viewed from the ventral aspect. The parts of the drawing round the sexual opening and the ovary have been made somewhat diagrammatic for the sake of clarity and the uterus is in actuality full of eggs. The vitelline and other fine ducts are not shown. The anterior extension of the ovary to the level of the sexual openings is not certain, since the ovarian follicles and vitellaria are in this region almost indistinguishable in my preparation.

Plate 25.

Caryophyllaeus filiformis.

Fig. 24 (×2).—Adult specimens.

Fig. 25 (×55).—Entire specimen magnified and viewed in optical section from the ventral aspect (the three parts of the figure should be continuous). The parts of the drawing round the sexual openings, and the ovary have been made somewhat diagrammatic for the sake of clarity and the uterus is in actuality full of eggs. The vitellaria and other fine ducts are not shown. The vitellaria in actuality surround the testes in the testicular region—vide fig. 28.

Fig. 26, *a*, *b*, *c*, *d*, *e* (×24).—Drawings showing variation in form of the head and the variable extension of the testes and vitellaria anteriorly.

Fig. 27 (×78).—Transverse section through the head region.

Fig. 28 (×78).—Transverse section through the testicular region.

Fig. 29 (×78).—Transverse section through the anterior uterine region.

Fig. 30 (×78).—Transverse section through the median isthmus of the ovary. The vagina has at this level become dorsal to the uterus.

Immature Caryophyllaeid from Auchenoglanis occidentalis.

Fig. 31 (×2).—The single specimen.

Fig. 32 (×35).—The external aspect of the specimen, viewed ventrally.